

# SUNRISE NEST ATTENTIVENESS IN COWBIRD HOSTS<sup>1</sup>

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**Abstract.** We recorded vigilance around sunrise at 140 nests of 10 potential host-species (six "accepters" and four "rejecters" of cowbird eggs) of the brood parasitic Brown-headed Cowbird (*Molothrus ater*) at Delta Marsh, Manitoba, to determine if hosts are present on or near their nests when cowbirds come to lay. We predicted that accepter species parasitized infrequently would be found to be more vigilant at their nests during this time than accepter species more heavily parasitized. During our watches we observed seven acts of parasitism, all between 03:44 CST (sunrise - 44 min) and 4:00 CST (sunrise - 25 min). We found no correlation between frequency of parasitism of accepter hosts and nest attentiveness. There was no significant difference between accepters and rejecters in early-morning vigilance. However, females of all species that roosted on their nests were more likely to be present during the critical period for parasitism than females that did not roost. Individuals that did not roost first arrived at their nests, on average, after cowbirds presumably would have arrived to lay and this difference was significant in six species. We suggest roosting on the nest may place the host in the best position to guard against parasitism, although this behavior does not always prevent parasitism.

**Key words:** Avian brood parasitism; Brown-headed Cowbird; *Molothrus ater*; pre-dawn laying; hosts; nest guarding; roosting.

## INTRODUCTION

Some hosts of Brown-headed Cowbirds (*Molothrus ater*) recognize female cowbirds as threats to their reproductive success and respond aggressively when they come near their nests (e.g., Robertson and Norman 1976, 1977; Smith et al. 1984; Neudorf and Sealy 1992). However, whether or not such behavior can reduce the chances that hosts will be parasitized has yet to be determined (e.g., Smith 1981, Smith et al. 1984). Experiments reveal that nest defense by birds may reduce predation (reviewed by Martin 1992), and where cowbird hosts nest densely, mobbing responses may lower parasitism rates (Robertson and Norman 1977). Furthermore, Arcese and Smith (1988) recorded a lower parasitism frequency at nests of Song Sparrows (*Melospiza melodia*) provisioned with food. This suggests the extra food allowed female sparrows to be more vigilant on their territories. Møller (1989) showed experimentally that nest guarding can reduce the frequency of conspecific brood parasitism in Barn Swallows (*Hirundo rustica*).

Regardless of the sophistication of a host's nest-defense system, nest owners would be expected to be vigilant and within striking distance of a parasite during the times when parasitism is most likely to occur, if they are to thwart parasitism. This is because parasites generally lay their eggs within just a few seconds (e.g., Chance and Hann 1942; Sealy et al., in press). Host aggression might prevent a cowbird from inspecting nests or removing a host egg prior to parasitism, but it is not known if such interference prevents parasitism from eventually occurring. Because these nonlaying visits by cowbirds occur over a large portion of the day (Mayfield 1961, Scott et al. 1992, Sealy 1992), the trade-off between nest guarding and time spent at other activities, such as foraging, would be expected to be more costly (e.g., Slack 1976, Arcese and Smith 1988). It should be more economical, therefore, for hosts to intercept cowbirds at their nests when the females come to lay, especially if laying occurs over the same few minutes each day.

A cowbird should lay when the host is away from the nest site, because a large host can sometimes injure a cowbird when it is near a nest (Leathers 1956). Scott (1991) suggested that cowbirds are most likely to lay their eggs early in the morning, when hosts begin to forage (see also Nolan 1978, Muma 1986). Indeed, Brown-headed Cowbirds lay their eggs a few minutes before sunrise (Harrison 1973, Scott 1991). Thus, po-

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tential hosts vigilant at their nests just before sunrise, during their egg-laying stages, should be in the best position to intercept a parasite.

A host could guarantee intercepting a cowbird by being on its nest when the cowbird comes to lay. However, almost nothing is known about the behavior of cowbird hosts at their nests around sunrise during the period when hosts are laying their eggs (but see Scott 1977). Some potential host species roost overnight in their nests beginning before or at the time they lay their first eggs (see Mueller et al. 1982, Brackbill 1985). These females would be in their nests before sunrise and thus might be able to defend their nests against parasitism.

Species that accept cowbird eggs laid in their nests, i.e., "accepters," would be expected to be more vigilant at their nests at sunrise than species that eject cowbird eggs from their nests, i.e., "rejecters" (Rothstein 1975), because cowbird parasitism is more costly for accepters than rejecters (Robertson and Norman 1976, Rohwer et al. 1989). Rejecter species may be better off being vigilant later in the day when cowbirds typically come to remove eggs.

Despite being good hosts, some acceptor species are seldom parasitized by cowbirds (e.g., Least Flycatcher *Empidonax minimus*, Briskie et al. 1990; Yellow-headed Blackbird *Xanthocephalus xanthocephalus*, Ortega and Cruz 1991). We hypothesized that these and other infrequently parasitized acceptor species may be more attentive at their nests during the time cowbirds normally lay than more frequently parasitized acceptor species. We also examined whether acceptor species were more likely to be vigilant at sunrise than rejecter species. We tested our hypotheses by quantifying the activity of 10 potential host species at or near their nests around sunrise.

## STUDY AREA

We conducted this research between 1974 and 1992 at Delta Marsh, Manitoba (50°11'N, 98°19'W), on the properties of the Portage Country Club, University of Manitoba Field Station, Municipality of Portage la Prairie, and Delta Waterfowl and Wetlands Research Station (see MacKenzie 1982, Neudorf 1991, Hill 1992 for descriptions of the study area). From 1974 to 1992, SGS recorded the frequency of natural parasitism on species in the host community. However, Red-winged Blackbirds (*Agelaius phoeni-*

*ceus*) were monitored only between 1986 and 1992 while Brewer's Blackbird (*Euphagus cyanocephalus*) and Yellow-headed Blackbird nests were monitored between 1989 and 1992. DLN and SGS conducted the nest-watches from mid-May through July, 1990–1992.

## METHODS

### FREQUENCY OF COWBIRD PARASITISM

We determined the 10 most common potential host species (see Table 1) available to cowbirds at Delta Marsh by intensively searching the ridge forest and interface between marsh and forest. We recorded nests in nearly all years for most species as they were initiated. We marked each nest nearby with numbered flagging tape and inspected most nests each day between about 07:00 and 12:00 (CST) before and throughout egg laying, but in some years only intermittently during the incubation and nestling periods. We calculated the percentage of parasitized nests of each species using all nests, including re-nests and second nests (in some years for some species) found before eggs appeared, host or cowbird, and those that failed before the host clutch was complete. We used parasitism frequencies for species that were determined over several years rather than just the years of our study because we expect selection for nest vigilance against cowbirds to operate over the long term. We may have underestimated parasitism frequencies for rejecters because in some cases cowbird eggs may have been removed before we checked a nest (Scott 1977). However, individuals of some species often take more than 24 hours to eject cowbird eggs experimentally placed in their nests (e.g., Eastern Kingbirds, *Tyrannus tyrannus*, Sealy and Bazin, in press; Gray Catbirds, *Dumetella carolinensis*, unpubl. data). In these species observed frequencies of natural parasitism may be more accurate than in Northern Orioles where eggs seem to be ejected almost immediately after parasitism (Rothstein 1977, Rohwer et al. 1989, see also Appendix).

### NEST-WATCHES

We observed six of the seven acts of parasitism described below while we watched nests of 10 potential host species around sunrise (from 03:30 to 04:30), when we expected cowbirds to visit nests to parasitize them (see Scott 1991). We watched most host nests on their second day of laying because up to that time the threat of par-

TABLE 1. Parasitism frequencies and time spent on the nest during the critical period (03:35 to 04:05 CST) by roosting and nonroosting females. Number of nests observed in parentheses.

Species <sup>1</sup>	Parasitism frequency <sup>2</sup>	Mean $\pm$ SE time on nest (min)		P <sup>3</sup>
		Roosting	Nonroosting	
Least Flycatcher (a)	2.9 (478)	12.0 (1)	0.0 (15)	
Eastern Kingbird (r)	0.01 (402)	30.0 (1)	2.0 $\pm$ 1.0 (12)	
American Robin (r)	4.4 (92)	18.9 $\pm$ 3.2 (11)	0.0 (1)	
Gray Catbird (r)	5.0 (101)	0.0 (0)	0.0 (9)	
Yellow Warbler (a)	19.1 (2,163)	27.6 $\pm$ 1.7 (12)	2.3 $\pm$ 1.6 (9)	0.0001
Red-winged Blackbird (a)	19.7 (213)	29.0 $\pm$ 1.0 (4) <sup>4</sup>	2.4 $\pm$ 1.0 (18)	0.0015
Yellow-headed Blackbird (a)	1.5 (67)	29.3 $\pm$ 0.4 (7)	4.4 $\pm$ 0.7 (11)	0.0003
Brewer's Blackbird (a)	37.0 (27)	0.0 (0)	0.0 (4)	
Common Grackle (a)	2.3 (44)	30.0 $\pm$ 0.0 (5)	0.0 (6)	0.0022
Northern Oriole (r)	3.3 (153)	30.0 (2) <sup>5</sup>	0.0 (9)	0.0028

<sup>1</sup> Hosts designated as "accepters" (a) or "rejecters" (r) after Rothstein (1975, 1977) but see Briskie and Sealy (1987) and Ortega and Cruz (1988) for verification of acceptor status in Least Flycatchers and Yellow-headed Blackbirds, respectively. Designation of Brewer's Blackbirds as accepters was on the basis of Friedmann et al. (1977).

<sup>2</sup> Parasitism frequencies determined from nests monitored at Delta Marsh, Manitoba, between 1974–1992 with the following exceptions: Red-winged Blackbirds (1986–1992), Yellow-headed Blackbirds and Brewer's Blackbirds (1989–1992).

<sup>3</sup> Results of Wilcoxon 2-sample test. Tests were not performed when sample sizes in either category were one or zero.

<sup>4</sup> Although 6 Red-winged Blackbirds roosted, 2 females that were accidentally flushed from their nests were not used in this analysis.

<sup>5</sup> One female Northern oriole was excluded from this analysis because her nest was parasitized while she was on it.

asitism is greatest (Rothstein 1975, Nolan 1978, Sealy 1992). If nests were parasitized prior to this stage we did not watch them. In addition to 24 Red-winged Blackbird nests observed, we watched one additional redwing nest in anticipation of it being parasitized, on the day the clutch was initiated. We also included an observation of parasitism at one of seven Clay-colored Sparrow (*Spizella pallida*) nests that Hill (1992) watched.

We set up a blind at each nest the night before the nest-watch and entered the blind the next morning just before 03:30. We determined, sometimes with a flashlight, whether the female was in the nest. In no instance did the light cause a roosting female to flush. Birds were twice accidentally flushed by the observers' approach. These nests were watched anyway and were used in the calculation of roosting frequencies, but not in the calculation of time spent nest guarding. We assumed that birds on their nests at this time had roosted there overnight (see Nolan 1978). Some birds might have left before 03:30 but we often started our watches 10 or 15 minutes earlier and never observed birds leaving prior to 03:30. If the female was in the nest, we recorded when she first left it, the number of subsequent times she visited the nest, and amount of time spent, if any, in the nest after roosting, until 04:30. If the female had not roosted in the nest, we recorded when she visited the nest and the length of time she spent in it. We also recorded the amount of time a parent was less than 5 m from

the nest. We considered nest-guarding to be occurring if at least one individual was within 5 m of the nest (including time spent on the nest).

Using Scott's (1991) method, we related the times cowbirds and hosts arrived at nests to sunrise (SR). To determine the exact time of sunrise at Delta Marsh for the days on which we observed parasitism, we used the 1991 "Observer's Handbook of the Royal Astronomical Society of Canada" (sunrise times for a given date exhibit little year-to-year variation in the temperate zone). We analyzed the data using nonparametric tests and all tests were two-tailed unless stated otherwise. We calculated standard error of the mean (SE) for all means.

## RESULTS

### PARASITISM EVENTS

We described the seven observations of parasitism at Delta Marsh in detail in the Appendix. The mean time of laying by Brown-headed Cowbirds was  $35.6 \pm 2.4$  (SE) min before sunrise (range: SR – 44 min to SR – 25 min,  $n = 7$ ). Female cowbirds flew silently and directly to or near the nests. Sometimes we detected the female when her wings fluttered or she rustled the vegetation. Cowbirds laid their eggs on average during  $63 \pm 12.3$  sec ( $n = 7$ ) spent on the nest, after which they flew silently and directly away.

In both cases when a host was present the cowbird laid despite being attacked. Both Clay-colored Sparrow parents managed to drive away the

TABLE 2. Mean ( $\pm$ SE) arrival times at nests of cowbirds and hosts, and time spent (mean  $\pm$  SE) within 5 m of the nest by hosts during the critical period (03:35 to 04:05 CST). Sample sizes are in parentheses<sup>1</sup>.

Species	Arrival time relative to sunrise (min)	Time within 5 m (min) <sup>2</sup>
Brown-headed Cowbird	SR - 35.6 $\pm$ 2.4 (7)	
Least Flycatcher	SR + 15.1 $\pm$ 6.8 (14)*	0.8 $\pm$ 0.8 (16)
Eastern Kingbird	SR - 9.4 $\pm$ 4.7 (12)*	4.2 $\pm$ 2.3 (13)
American Robin	SR - 14.0 (1)	20.9 $\pm$ 2.9 (12)
Gray Catbird	SR + 15.1 $\pm$ 12.6 (9)*	0.0 (9)
Yellow Warbler	SR - 21.8 $\pm$ 4.0 (9)*	17.9 $\pm$ 2.8 (21)
Red-winged Blackbird	SR - 31.3 $\pm$ 2.7 (18)	11.1 $\pm$ 2.2 (22) <sup>3</sup>
Yellow-headed Blackbird	SR - 29.6 $\pm$ 3.6 (11)	14.7 $\pm$ 3.4 (18)
Brewer's Blackbird	SR - 15.5 $\pm$ 10.5 (4)*	0.5 $\pm$ 0.5 (4)
Common Grackle	SR - 18.8 $\pm$ 13.1 (6)	13.7 $\pm$ 4.7 (11)
Northern Oriole	SR + 0.9 $\pm$ 11.5 (9)*	8.6 $\pm$ 4.1 (12)

<sup>1</sup> Sample sizes differ between columns because arrival times include only the number of nests at which the female did not roost, while time within 5 m includes all nests watched.

<sup>2</sup> Time at least one individual was within 5 m of the nest and includes time spent on nest.

<sup>3</sup> Does not include two nests at which the females were accidentally flushed at the beginning of the watch.

\* Differed significantly from cowbird arrival time (Wilcoxon 2-sample test,  $P < 0.05$ , one tailed).

female cowbird on her first attempt at parasitism but not on her second attempt. Only once was a female host, a Northern Oriole (*Icterus galbula*), on her nest when the cowbird approached. The cowbird entered the nest despite the oriole's presence and, although a fight ensued within the nest, the cowbird still laid her egg. In the second oriole nest where we observed parasitism, the female oriole arrived at her nest and struck the cowbird just as she was leaving the nest. The four observations of parasitism on Red-winged Blackbirds occurred in the absence of the nest owners.

#### SUNRISE NEST-GUARDING

The tendency of hosts to roost in the nest before sunrise was not an all-or-none phenomenon. Roosting frequencies ranged among species from 0% (Gray Catbirds, Brewer's Blackbirds) to over 90% (American Robins, *Turdus migratorius*). Eastern Kingbirds and Least Flycatchers both roosted infrequently while 25% to over 50% of individuals of the remaining five species spent the night in their nests. There was no significant correlation between parasitism frequency and tendency of females of the 6 acceptor species to roost on their nests (Spearman rank correlation,  $r_s = -0.49$ ,  $P = 0.33$ ). Furthermore, acceptor species were not more likely than rejecters to roost on their nests (Wilcoxon 2-Sample Test,  $Z = -0.12$ ,  $P = 0.91$ ).

The seven acts of parasitism we observed all occurred between 03:44 and 04:00. Thus, we defined a "critical period" during which hosts should be expected to be near their nests to have the

best opportunity to prevent parasitism. We analyzed host presence over 30 min from 03:35 to 04:05, within which parasitism at Delta Marsh was most likely to occur. There was no significant correlation between time spent nest guarding during the critical period and parasitism frequency for the acceptor species (Spearman rank correlation  $r_s = -0.54$ ,  $P = 0.27$ ). Acceptor species did not spend more time guarding their nests during the critical period than did rejecter species (Wilcoxon 2-Sample Test,  $Z = -0.32$ ,  $P = 0.75$ ).

However, in all species, females spent more time on their nests during the critical period if they had roosted on their nests the previous night compared with individuals that had not roosted (Table 1). Over 62% ( $n = 43$ ) of the females that roosted on their nests did not leave their nests before the end of the critical period and of those individuals that left early, 31% returned to their nests before the end of the critical period. Adults spent little time guarding during the critical period, i.e., if females had not roosted on the nest they likely were not in the nest area at all (Tables 1, 2). Hosts that did not roost first arrived at their nests, on average, after cowbirds' expected laying times; this difference was significant in six of the 10 species (Table 2).

#### DISCUSSION

The seven observations of cowbird parasitism provide convincing evidence that female cowbirds have located ahead of time nests for parasitizing (see also Friedmann 1929, Norris 1944,

Mayfield 1960, for descriptions of cowbird behavior during laying). Their direct flight to nests in the dim light before sunrise, without vocalizing, and very rapid laying and departure, suggest female cowbirds try to parasitize nests unnoticed by the hosts. If such behavior evolved in response to host vigilance and nest defense, then it is likely that hosts occasionally thwart parasitism attempts.

Rarely parasitized acceptor species were not more attentive to their nests at sunrise than those more heavily parasitized (Table 2). The low frequency of parasitism on Least Flycatchers, for example, cannot be attributed to intensive early-morning vigilance. This species was consistently away from its nest during the critical period and yet it was infrequently parasitized. Individuals may have been more than 5 m from their nests, and out of our sight, but they still may have been able to defend their nests. However, Slack (1976) determined that Gray Catbirds must be within 5 m of the nest to be considered to be nest guarding, based on Zimmerman's (1963) observations that male catbirds usually guard within a few meters of the nest. We predicted that for hosts to prevent a cowbird from laying, they should be close to the nest, or in it, guarding it in the minutes of low light before sunrise.

As cowbird parasitism threatens the genetic parentage of both foster parents, it should pay both sexes to guard the nest and repel cowbirds. However, we did not detect in any species a system of nest guarding coordinated between males and females that kept at least one adult near the nest during the critical period. Slack (1976) reported that after an incubation bout, female Gray Catbirds signaled to their mates when they left the vicinity of the nest. While the females foraged, male catbirds remained near the nests, and Slack speculated that this was to prevent predators or brood parasites from approaching. Smith (1966) reported a coordinated nest guarding system for Eastern Kingbirds during incubation, but he did not look for it during egg laying. We suggest such a system may be less important at nests where females roosted and remained in the nests during the critical period.

Birds that did not roost in their nests also did not guard their nests during the critical period. These nonroosting individuals generally arrived at their nests after cowbirds would have laid (Table 2). Therefore, we suggest that being in the nest at dawn may be the best position for cowbird

hosts to prevent parasitism. To our knowledge there is no evidence that cowbirds actually force hosts off their nests (but see Hann 1937, Prescott 1947). In fact, female Yellow Warblers (*Dendroica petechia*) rush to their nests and sit in them in response to a female cowbird model placed nearby (Hobson and Sealy 1989). This suggests nest sitting may be an effective defense against cowbirds. Benson (1939:124) reported an American Redstart (*Setophaga ruticilla*) that sat tightly on its nest at the approach of a female cowbird; the cowbird eventually left without flushing the redstart. However, this visit was well after the usual hour of parasitism.

Although more than half of the Yellow Warblers in our study roosted in their nests, remaining in them on average 28 min during the critical period, the Yellow Warbler was one of the most heavily parasitized species on our study area (Table 1). Possibly, individuals within a species that roost in their nests are the ones that avoid being parasitized. One way to test this hypothesis would be to compare parasitism frequency of individuals that roosted and those that did not roost; however, our sample sizes of parasitized individuals were not sufficient to test this hypothesis. In fact, we did not observe any instances of parasitism on Yellow Warblers during our watches. One reason for this may be that Yellow Warblers are most often parasitized by cowbirds before they have laid their second eggs (see Sealy 1992). Future research should include watches at host nests before the second eggs have been laid to determine the stage when roosting begins.

Another explanation for the frequent parasitism on Yellow Warblers may be that cowbirds can easily evict small hosts from their nests, but not larger ones such as American Robins, Yellow-headed Blackbirds, or Common Grackles (*Quiscalus quiscula*). In support of this, many females of the larger species roosted in their nests, and they were parasitized infrequently (Table 1), as we predicted. Some parasitic ducks force nest owners off their nests or push themselves beside the sitting female and then lay (McKinney 1954, Nudds 1980). Wood Ducks (*Aix sponsa*) parasitizing conspecifics occasionally encounter the nest owner in a nest box, and this generally results in a fight (Clawson et al. 1979). Parasites should be better off avoiding such encounters because they might injure themselves, damage their own eggs, or cause the nest to be deserted (Sealy et al., in press). However, in hosts that

nest in cavities or build covered nests, parasites may not know whether the nest owner is present until after entering the nest.

Ricklefs (1969) suggested that selection should favor cowbird hosts that exhibit increased tenacity to the nest during the stages most vulnerable to parasitism. Even though cowbirds parasitize nests during a predictably brief period each day, many host individuals left their nests unprotected at this time. If small hosts cannot physically exclude cowbirds from their nests, avoiding their nests as much as possible may minimize the likelihood of advertising their location (Burgham and Picman 1989), even though cowbirds have discovered them on a previous day.

Acceptor species were not more vigilant at their nests than rejecter species during the critical period for parasitism. Since there can be costs associated with ejecting cowbird eggs (see Rothstein 1977, Rohwer et al. 1989) rejecter species also could benefit from preventing parasitism by guarding their nests. However, regardless of acceptor/rejecter status, for some hosts guarding at this time of day may conflict with other activities such as foraging, singing (especially in males), or territorial maintenance.

Why some seemingly good hosts are parasitized rarely still remains a mystery. Differences in early morning vigilance cannot fully account for the observed differences in parasitism frequencies of hosts. Furthermore, the effectiveness of nest defense, particularly in small hosts, is still in question. Future studies should focus on frequently parasitized hosts such as Yellow Warblers and Red-winged Blackbirds to determine the onset of roosting behavior and whether nest-sitting prevents parasitism.

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## APPENDIX

## OBSERVED ACTS OF PARASITISM

The act of oviposition by Brown-headed Cowbirds has been witnessed directly and mentioned or described in the literature a total of 21 times (see review in Scott 1991). All of these parasitism events took place in the Great Lakes region of northeastern North America, and involved 11 host species. Below are descriptions of seven laying events of cowbirds we observed during nest-watches at Delta Marsh, which involved four parasitisms on Red-winged Blackbirds, two on Northern Orioles, and one on a Clay-colored Sparrow. Cowbird parasitism on these species has not been witnessed previously.

*Red-winged Blackbird.* Nest 1. The first egg was laid on 1 June 1991. At 03:20 on 2 June, S. A. Gill flushed a female blackbird from the nest, and neither she nor any other blackbird was seen near the nest from 03:30 through 03:44. At 03:44 (SR - 44 min), a female cowbird rustled dead reeds (*Phragmites communis*) as she entered the nest. The cowbird remained on the nest for about 60 sec while laying, and then flew directly away. She was silent as she approached the nest and during the entire laying event. The nest was watched until 05:46. Although a male and female blackbird moved about near the nest during this period, and once a female came within less than 1 m of the nest, the female blackbird did not lay in the nest on that morning, or on a subsequent morning, indicating the nest had been deserted.

Nest 2. Placed in a small clump of reeds along a ditch, another blackbird nest received its first host egg on 5 June 1991. On 6 June the nest contained no eggs and DLN did not see any blackbirds near it between

03:30 and 03:46. At 03:46 (SR - 39 min), a female cowbird was detected as she rustled through reeds upon entering the nest where she laid her egg within 40 sec. The cowbird did not vocalize as she arrived at the nest, during laying, or when she departed. Adult blackbirds were not seen near the nest until 04:05 when a male sang for 2 min, about 5 m away. Between 04:21 and 04:43, a male and female blackbird intermittently perched 2-5 m from the nest, and once, at 04:45, a female entered the nest but left it about 1 min later. A female entered the nest at 04:53 (SR + 28 min), this time to lay her second egg, and left at 05:15. This nest eventually received a full clutch of eggs but its outcome was unknown.

Nest 3. Placed in new growth of *Phalaris arundinacea*, this nest received its first egg on 23 June 1991. From 03:28 to 03:52 on 24 June, a male blackbird called once about 10 m from the nest. At 03:52, DLN saw a female cowbird fly in and land 1 m from the nest, perch there for 20 sec before entering the nest (SR - 30 min) to lay during the 94 sec she spent on the nest. The cowbird flew directly away from the nest, and did not vocalize at any time. DLN watched the nest until 05:41, and although a male and female blackbird perched several times and called within 5 m of the nest, and once the female entered the nest, apparently no egg was laid that day, although the cowbird might have later removed an egg. At 08:30, the nest contained one egg each of the cowbird and blackbird, but by 17:38 only a cowbird egg was present. This nest did not receive any more eggs and was abandoned.

Nest 4. Supported by dead stems of *Typha latifolia* amid *Phalaris arundinacea*, this nest received a cowbird egg on 1 June 1992, and at 07:48 SGS removed it for another experiment. At 03:30 on 2 June, SGS recorded that the female blackbird was not on the nest, and no blackbirds were seen or heard near the nest until 03:36 when a male flew by 5 m from the nest, calling twice. At 03:48 a male blackbird chased a female cowbird at least 5 m above and beyond the nest, until they were both out of sight. At about 03:51, a female cowbird flew in and landed on a reed 4-5 m from the nest, where she perched for 19 sec. She then flew down to the ground behind vegetation, stayed there for 9 sec, out of sight, and then for the next 7 sec walked several cm toward the nest, often out of sight, hopped up and down for a few seconds, and entered the nest at 03:52 (SR - 37 min). The cowbird laid her egg during the 33 sec she spent on the nest. She then flew directly away from the nest, without ever vocalizing. Between 04:02 and 04:50, the female blackbird frequently changed perches 2-5 m from the nest, and twice visited the nest each time for only a few seconds at 04:45 and 04:47. Finally, the female blackbird entered the nest at 04:50 (SR + 23 min) and laid her own egg over the next 10 minutes. The female completed a clutch of 5 eggs on 6 June, and the cowbird and four host young eventually fledged.

*Northern Oriole.* Nest 1. This nest (height 5 m) received its first oriole egg on 7 June 1991. At 03:26 on 8 June, DLN determined that the female oriole was in the nest, but she did not detect the male until 03:37 when he began a 3-min singing bout, perched more than 5 m from the nest. At 03:47 (SR - 38 min), a female

cowbird entered the nest even though the female oriole was in it. The nest immediately shook as the two birds fought violently, with the oriole screaming continuously during the 119 sec the cowbird was in the nest. Nevertheless, the cowbird laid her egg during this time and then flew directly away, without ever vocalizing. The female oriole remained in the nest until 04:08 and then perched near it for more than 1 min before flying back to the nest's edge where she twice probed the eggs with her bill. A few seconds later, the oriole again thrust her head into the nest and came up with the punctured cowbird egg impaled on her mandibles. She flew away with the egg, but dropped it within a few meters. The female oriole entered the nest again at 04:12 but left about 1 min later. Over the next 110 min, until the female oriole finally entered the nest to lay her own egg, the male and female orioles often perched within 5 m of the nest, the male occasionally singing and foraging, while the female sometimes foraged and preened. Once the female entered the nest and removed a piece of vegetation. At 06:03 (SR + 98 min), the female oriole entered the nest and during the next 46 min she laid her egg. The oriole added four more eggs to the clutch, and young eventually fledged.

Nest 2. About 4 m high and supported by the main stem of a *Salix interior*, this nest received its first oriole egg on 5 June 1992. On 6 June, when DLN arrived at 03:25 to begin the nest-watch, the female oriole was not in the nest. Between 03:25 and 03:56, an oriole twice called, more than 5 m from the nest, but was not seen. At 04:00, a female cowbird flew to the nest, put her head into it, and then perched for 5 sec, 2 m away before entering the nest (SR - 25 min). She left the nest 35 sec later after laying her egg. The female oriole struck the cowbird as she left the nest and flew away, but did not pursue her. Instead, the female oriole entered the nest but about 1 min later left it and perched nearby. Over the next 75 min, the female oriole entered and left the nest repeatedly and at 05:26 carried away the cowbird egg. Over the next 139 min, until observations ceased, the female oriole five times added nest material to the body and lining of the nest, but never laid her second egg that day, or the next. On 8 June the oriole laid the second of a five-egg clutch that was completed on 11 June. Young eventually fledged from the nest.

*Clay-colored Sparrow.* At 03:42 on 22 June 1991, D. P. Hill flushed a Clay-colored Sparrow off a nest that contained two host eggs. At 03:45, a female cowbird landed on the ground 10 m from the nest, and less than 1 min later she flew toward the nest where she was attacked by a sparrow uttering alarm calls. By 03:47 the sparrow had chased the cowbird out of sight, but the cowbird returned within seconds and entered the nest (SR - 36 min), attacked now by two sparrows. Sixty seconds later, after laying an egg, the cowbird flew directly away from the nest, chased by a sparrow, which suddenly stopped, perched, and began to sing. A sparrow then repeatedly entered and left the nest over the next 97 min, until 05:24 (SR + 61 min), when the female finally entered and remained on it for 24 min and laid her egg. Although the sparrows accepted the cowbird egg, and the female sparrow laid one more egg of her own, the nest eventually was preyed upon.